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APPLICATION OF METAPOPOPULATION THEORY TO NORTHERN BOBWHITE CONSERVATION

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) populations have declined throughout the majority of the species' range, and have experienced the largest declines in fragmented habitats, suggesting landscape scale processes may be responsible for this decline. We used the results from a stochastic population dynamics model of South Texas bobwhites as conceptual justification for use of metapopulation theory in bobwhite management. Annual quasi-extinction probabilities for isolated bobwhite populations were 0.003 (95% CI: 0.001–0.006), 0.105 (95% CI: 0.083–0.126), and 0.773 (95% CI: 0.750–0.796) for simulated populations harvested at 20, 30, and 40% annually. The probability of regional persistence at 30% harvest increased to ~ 100% in scenarios where we modeled 5 occupied hypothetical 800-ha habitat patches; however, at 40% harvest rates, probability of regional metapopulation persistence did not reach 95% until 12 habitat patches were occupied. This suggests bobwhites probably require somewhere from 800 to 9,600 ha of available habitat space to maintain 95% probability of regional metapopulation persistence as harvest varies from 0 to 40% annually. Our results have strong implications for bobwhite harvest management given the high probability of quasi-extinction of isolated populations at rates of harvest $\geq 25\%$. Multiple patches of habitat (where individual patch size is ≥ 800 ha) must be available to ensure bobwhite metapopulation persistence.

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Key words: *Colinus virginianus*, dispersal, metapopulation dynamics, northern bobwhite, simulation modeling

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INTRODUCTION

The long-term range-wide decline in northern bobwhite populations has been occurring since the late 19th Century, and has been a concern of research scientists and quail managers since at least the 1930s (Stoddard 1931, Brennan 1991). This decline is primarily associated with landscape-scale fragmentation and range-wide loss of usable habitat space (Brady et al. 1998). Habitat fragmentation has broad scale implications for impacting ecosystem processes, and maintaining native biodiversity (Saunders et al. 1991, Walters 1998, Fahrig 2003), of which northern bobwhites and their habitat are clearly a part.

Metapopulation theory is based on the concept of individuals dispersing from one population to another and these movements have an impact on the probability of persistence of the entire metapopulation (Hanski 2001). Bobwhites have generally been considered a sedentary species; however, observations from banded and radio-marked bobwhites (Lehmann 1984:119, Fies et al. 2002, Townsend et al. 2003, Cook et al. 2009) and genetic analysis from Texas (R. W. DeYoung, unpublished data) indicate bobwhite dispersal among habitat patches may occur more frequently than previously thought.

Bobwhites have been subject to intense research efforts since the 1920s, but little is known about the potential applicability of metapopulation theory in northern bobwhite conservation. Our objectives were to: (1) use the results from a stochastic bobwhite population dynamics model developed for the South Texas Plains as the basis for a classical (Levins 1970) metapopulation modeling exercise using 5 simulated harvest scenarios; (2) apply these results as conceptual justification for application of metapopulation theory in bobwhite management; and (3) discuss how the metapopulation concept is consistent with habitat objectives necessary for successful bobwhite conservation outcomes at local, state, and national scales.

METHODS

Field Methods

We collected field data (DeMaso 2008, Sands 2010) in the South Texas Plains ecoregion (Gould 1975). The South Texas Plains experiences high annual and seasonal variability in rainfall amount, and quail populations exhibit irruptive population behavior (Lehmann 1984). The study area was on private rangeland in Brooks County, Texas. Land uses on the study area included wildlife management for commercial hunting, primarily bobwhite and white-tailed deer (*Odocoileus virginianus*), and cattle production, as well as oil and natural gas production. Bobwhite hunting on the study sites was conducted by following dogs from vehicles.

Historical accounts of the region vary greatly (e.g., barren desert or lush grassland) due to high variation in rainfall, and depending on conditions at the time (Lehmann 1984). The study area was in a landscape

composed predominantly of suitable quail habitat. The plant community was a mixed-brush community characteristic of the South Texas Plains (McLendon 1991). Common brush species included mesquite (*Prosopis* spp.), huisache (*Acacia farnesiana*), granjeno (*Celtis pallida*), and brasil (*Condalia hookeri*) (Everitt et al. 2002), and Texas prickly pear (*Opuntia lindheimeri*) (Hatch and Pluhar 1993). Common forbs included dove-weed (*Croton* spp.) and sunflower (*Helianthus* spp.) (Everitt et al. 1999). Common grasses were seacoast bluestem (*Schizachyrium scoparium*), gulf cordgrass (*Spartina spartinae*), sandbur (*Cenchrus incertus*), and purple threeawn (*Aristida purpurea*) (Gould 1978). Sands (2010) provided detailed information regarding the study area.

Analyses

We used the harvest-population dynamics model developed by Sands (2010) to evaluate the probability of quasi-extinction (Guthery et al. 2000, DeMaso et al. 2011) for isolated populations of northern bobwhites at 0, 20, 25, 30, and 40% annual harvest rates. This represented a stochastic population dynamics model that estimated probability of population persistence under harvest rates ranging from 0 to 40%. The model followed the general approach of DeMaso et al. (2011) and Rader et al. (2011) where bobwhites were produced during the spring and summer, and were removed as a result of natural mortality during each season. The model represented a bobwhite population on a hypothetical property of 800 ha. Our model consisted of stocks (chick, juvenile, and adult bobwhites), flows (transfer of chick, juvenile, and adult bobwhites into or out of the model), and auxiliary variables (e.g., mortality rates, reproduction) that influenced flows. Harvest of bobwhites was considered to be partially additive to natural mortality based on the additive harvest model (Ricker 1958, Roseberry 1979, Guthery 2002:100). We conceptualized (Fig. 1) and programmed our model using STELLA Version 9.0 (ISEE Systems, Lebanon, NH, USA). Sands (2010) provides explicit details on model development and quantification.

We simulated the dynamics of the population and evaluated its probability of persistence for each harvest scenario over a 100-year period. Stochasticity was invoked during each 100-year simulation by randomly selecting values for production and survival from empirically derived Weibull probability distributions generated within SAS 9.1 (SAS Institute Inc., Cary, NC, USA). We used normal distributions for stochastic variables when Weibull parameters could not be estimated (DeMaso et al. 2011).

We conducted 50 preliminary stochastic baseline simulations to obtain variance estimates for the parameters: winter (hunted) population, winter (hunted) density, spring (post-hunt) population, spring (post-hunt) density, and harvest. We conducted 165 simulations for each level of harvest (0, 20, 25, 30, and 40%) because it was the largest number of simulations considered necessary to achieve our

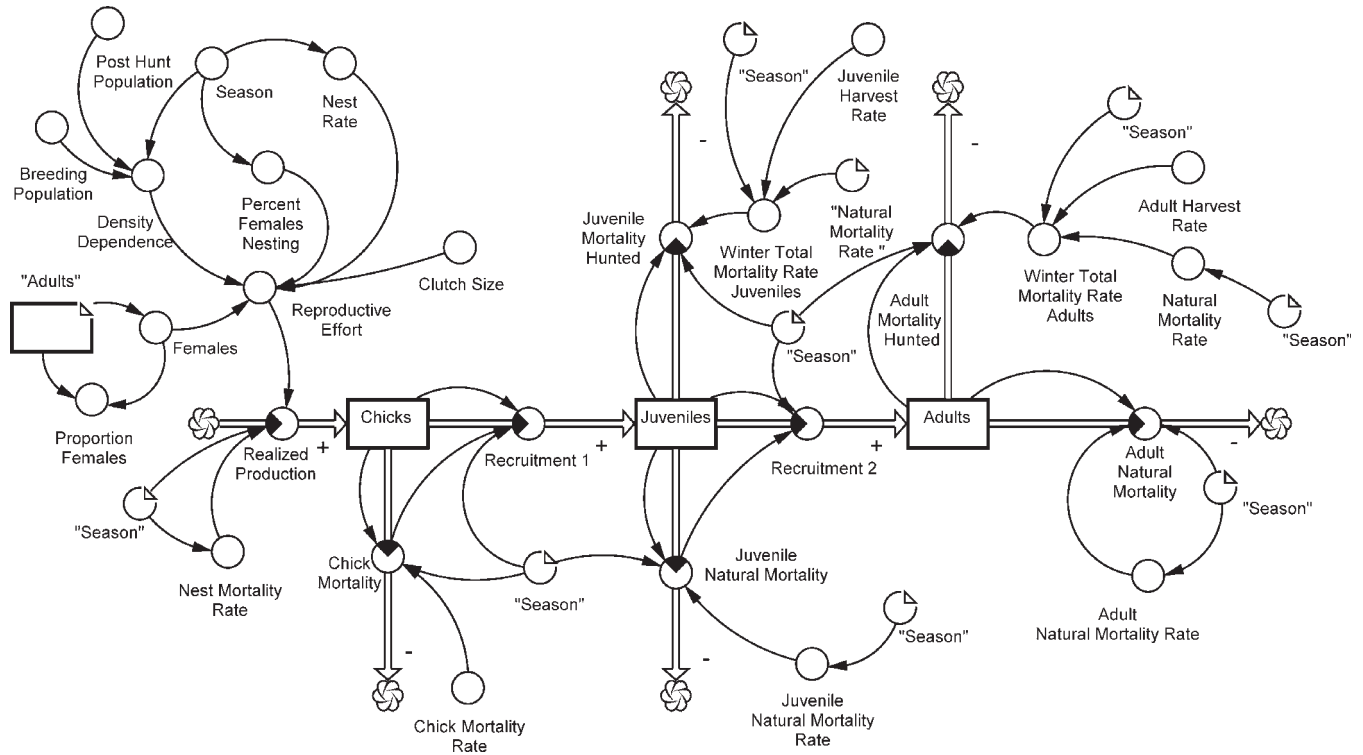


Fig. 1. Conceptual model of factors impacting northern bobwhite population dynamics in the South Texas Plains (Sands 2010). Boxes are variables which represent stocks of northern bobwhites at different age classes (chicks, juveniles, and adults). Circles represent driving variables, auxiliary variables and/or constants (e.g., natural mortality rates, density-dependence, harvest rates). Large arrows with centered circles represent flows. Flows transfer material into (+) or out of (–) state variables (e.g., production and mortality).

objectives for model power (DeMaso et al. 2011), based on the formula provided by Sokal and Rohlf (1969:247) and Grant et al. (1997:61–64). We set our quasi-extinction level at 0.05 bobwhites/ha (40 bobwhites, based on DeMaso et al. 2011) and calculated the probability of quasi-extinction for each 100 year simulation as:

$$P_{qe} = \frac{n_{qe}}{100} \quad (1)$$

where,

P_{qe} = probability of quasi-extinction in a given year, and

n_{qe} = number of quasi-extinctions per 100 year simulation.

We used the spatially implicit model developed by Levins (1970) to model the probability of local population persistence as:

$$P_n = (1 - p_{qe})^n \quad (2)$$

where,

P_n = probability that a population will exist for n years, and

p_{qe} = annual probability of local quasi-extinction.

We also modeled the probability of regional persistence (the probability that all patches within the metapopulation do not go simultaneously extinct):

$$P_x = 1 - (p_{qe})^x \quad (3)$$

where,

P_x = probability of regional persistence in a metapopulation, and

x = the number patches in the metapopulation.

Equation 3 does not assume that immigration or emigration occurs among patches. Instead, it predicts the probability that all patches within the metapopulation do not go simultaneously extinct (Gotelli 2001).

We calculated the mean and 95% confidence intervals for P_{qe} , P_n , and P_x based on 165 simulations for each harvest scenario (0, 20, 25, 30, and 40% annual harvest).

RESULTS

The baseline model (no annual harvest) indicated a 100% probability of population persistence (0.0 probability of quasi-extinction) for a simulated isolated bobwhite population. Annual quasi-extinction probability at a 20% annual harvest rate was 0.003 (95% CI: 0.001–0.006) and was 0.105 (95% CI: 0.083–0.126) at a 30% annual harvest rate. Annual probability of quasi-extinction increased to 0.773 (95% CI: 0.750–0.796) for a simulated population harvested at 40% annually.

The simulated population maintained a 95% probability of persistence for 15 years at a 20% annual harvest rate, whereas a simulated population at a 30% annual harvest rate had only a 33% probability of persisting for 10 years (Fig. 2). Isolated populations had a < 1 probability of persisting for 5 years, given a 40% annual harvest rate (Fig. 2).

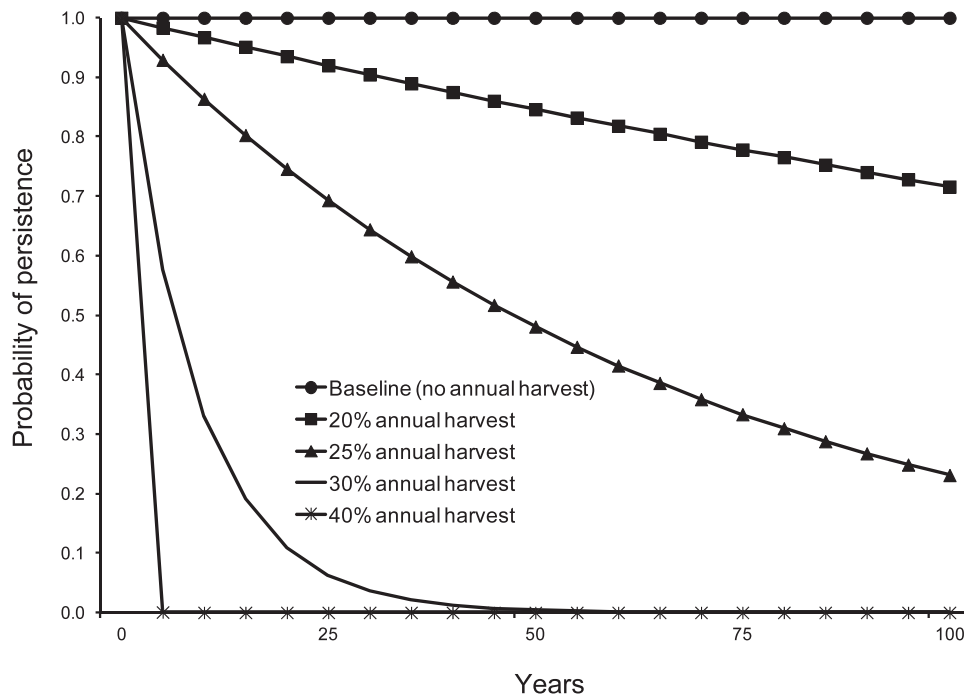


Fig. 2. Simulated 100-year probability of population persistence of an isolated South Texas Plains northern bobwhite population at 0, 20, 25, 30, and 40% harvest rates.

A regional bobwhite metapopulation persisted with relative certainty from baseline to 30% harvest rates given at least 1 (baseline, no annual harvest), 2 (20% harvest, 25% harvest), or 3 (30% harvest) habitat patches (Fig. 3A–C). The regional population did not reach 95% probability of persistence at a 40% harvest rate (Fig. 3D) until 12,800 ha of occupied habitat patches existed (Table 1).

DISCUSSION

Harvest and Bobwhite Metapopulation Persistence

Our simulation results were based on data collected within the South Texas Plains ecoregion (DeMaso 2008, Sands 2010, DeMaso et al. 2011). These results suggest at a minimum, given our hypothetical area of 800 ha, bobwhites require from 800 to 9,600 ha of available habitat space to maintain a 95% probability of regional metapopulation persistence as harvest rate varies from 0 to 40% annually. The South Texas Plains represents a relatively broad and contiguous landscape comprised of suitable bobwhite habitat, much of which persists as a direct result of management targeted directly for bobwhites. The Sands (2010) model indicated increasing populations based on estimates of finite rate of increase ($\lambda > 1$) for annual harvest rates up to 30%. Our results may not apply directly to other ecoregions where habitat fragmentation is more widespread or where harvest pressure is, on average, $> 30\%$. However, the potential implications of our results for other portions of the bobwhite range are significant because they suggest multiple-patch habitat connectivity is necessary, especial-

ly when harvest pressure is relatively high. It is likely a greater number of habitat patches would be necessary to maintain a high probability of regional metapopulation persistence for declining populations in fragmented habitats subjected to consistently high harvest pressure (e.g., $> 30\%$ harvest annually).

Harvest pressure (e.g., hunter-days as a function of abundance) may increase as population abundance decreases (Guthery et al. 2004). Isolated populations (e.g., populations that are separated (~ 3 – 5 km) by a barrier that may impede, but not totally restrict, dispersal) in small habitat patches are more likely to be small. Thus, harvest may have little impact on northern bobwhite populations at large landscape scales (e.g., $\geq 1,000,000$ ha), but it has potential to impact abundance and population persistence at the ranch or pasture scale (~ 800 – $2,000$ ha), especially if dispersal among patches is inhibited by unsuitable habitat space.

Dispersal is one of the least studied aspects of northern bobwhite life history (but see Fies et al. 2002, Townsend et al. 2003, and Cook et al. 2009 for exceptions). However, it seems apparent that bobwhites are neither high dispersers nor are they sedentary. Bobwhite dispersal rates range from 25 to 41% (Fies et al. 2002, Townsend et al. 2003, Cook et al. 2009), and application of metapopulation theory to northern bobwhite management is theoretically appropriate. The metapopulation paradigm is consistent with the usable space hypothesis (Guthery 1997) and shows consistency with results of landscape genetics studies from South Texas (R. W. DeYoung, unpublished data).

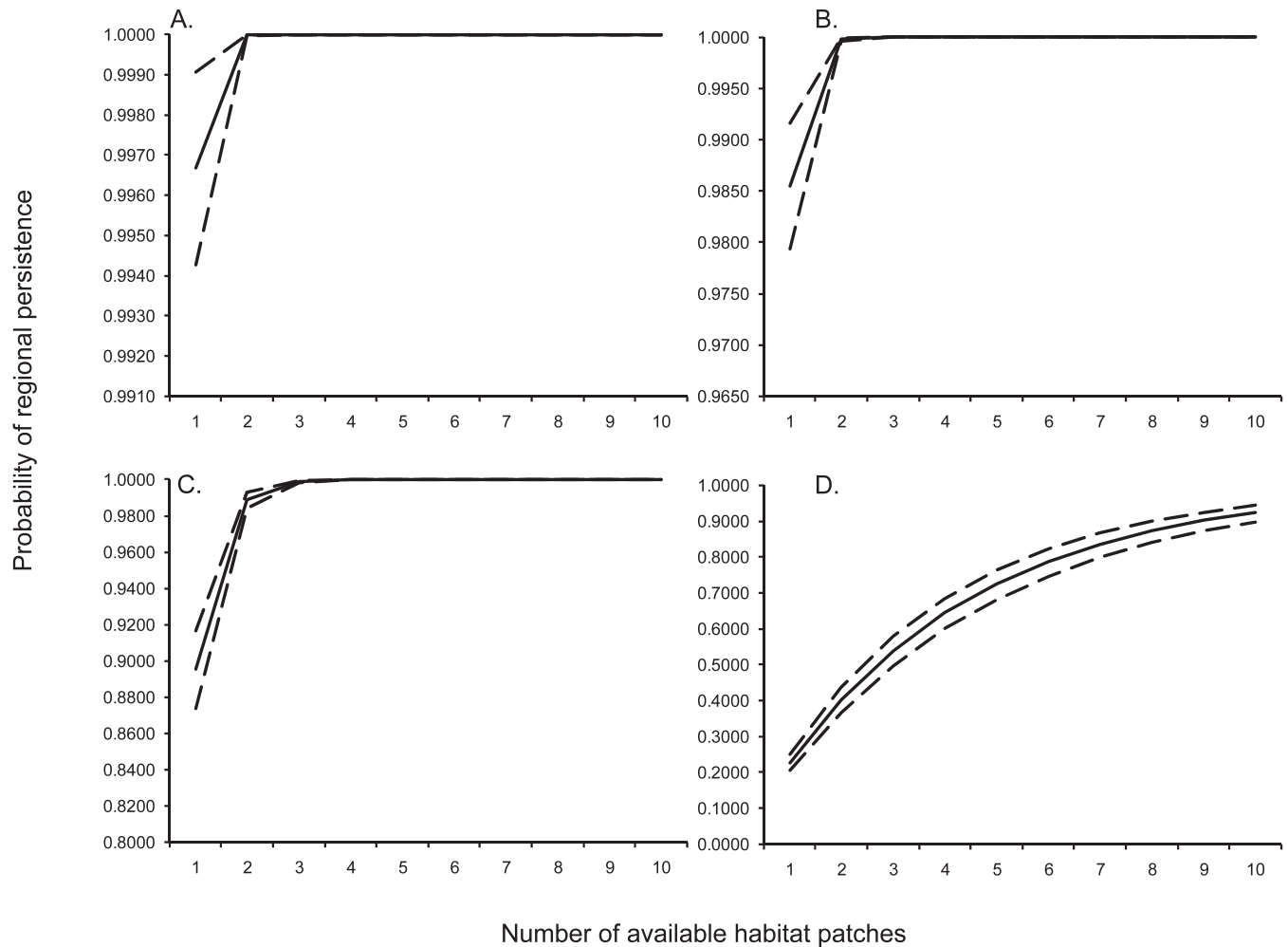


Fig. 3. Simulated probability of regional persistence for a northern bobwhite metapopulation in the South Texas Plains at (A) 20, (B) 25, (C) 30, and (D) 40% harvest rates. Dashed lines represent upper and lower 95% confidence intervals of population persistence.

A Call for Changing Research Priorities

Bobwhite populations have undergone a range-wide decline in abundance since at least the late 19th century and perhaps even earlier. The number of suitable bobwhite habitat patches has also decreased through landscape scale habitat loss. Thus, it is reasonable to assume the proportion of remaining suitable habitat patches occupied by bobwhites has also decreased. Our results represent a first approximation of how spatially implicit classical metapopulation models (Levins 1970, Gotelli 2001) can be applied to bobwhite population dynamics. Spatially explicit models will be necessary to move our understanding of bobwhite metapopulation and landscape ecology from theoretical to empirical.

Research that focuses on quantifying the spatial and temporal aspects of bobwhite dispersal as related to landscape characteristics, and the dynamics of density and weather, would represent a step forward in improving knowledge of bobwhite ecology. Models that incorporate a suite of parameters including rates of dispersal (immigration and emigration) should prove useful in

evaluating northern bobwhite metapopulation dynamics for specific regions. Metapopulation theory is applicable to bobwhite biology. These parameters have large implications for bobwhite population dynamics. Researchers must first identify multiple habitat patches within a landscape and obtain a sufficiently large sample of bobwhites to estimate dispersal among patches. Long-term (e.g., ≥ 10 year) studies would be invaluable for learning about individual patch and metapopulation

Table 1. Number and area (ha) of available habitat patches necessary to sustain a 95% probability of population persistence of a simulated bobwhite metapopulation in the South Texas Plains ($n = 165$, 100-year simulations).

Annual harvest rate	Available habitat patches	Area (ha)
Baseline (no annual harvest)	1	800
20–25%	2	1,600
30%	3	2,400
40%	12	9,600

dynamics. The majority of current bobwhite research does not address these issues, despite the existence of quantitative methodology and GIS technologies that make doing so possible.

MANAGEMENT IMPLICATIONS

Bobwhite conservation will be more effective if implemented at spatial scales consistent with bobwhite population processes; this would allow managers to prioritize biologically meaningful habitat conservation and restoration efforts. Viable bobwhite populations need large patches of habitat that are connected on a landscape scale. Managers should recognize individual blocks of habitat (e.g., 800–1,500 ha) may represent only one of several patches within a metapopulation network. Thus, processes such as metapopulation dynamics and dispersal among habitat patches should be considered when designing conservation strategies.

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